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Review

The Cambrian fecal revolution: Fueling the Cambrian Radiation

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Coprolites—fossil material extruded from an animal's digestive system—represent a rare insight into trophic interactions in deep time. However, while the first animals appeared about 600 million years ago, the first coprolites are only observed in the earliest Cambrian. Conversely, in modern oceans, fecal pellets are an important part of the particulate organic carbon in the water column and the global flux of organic carbon to deep water. In this review, we analyze the impact of the advent of fecal matter on the Cambrian Radiation by examining coprolites, analyzing animal biology, and contextualizing this through the role of fecal pellets in the oceanic nutrient cycle. We illustrate the central position of coprolites in driving the Cambrian Radiation.

Highlights

The 'Cambrian Radiation' comprises the rapid diversification of marine organisms and ecological niches during the Ediacaran to Cambrian Periods. It is also the time during which animals with guts first appear. The appearance of guts, in turn, leads to fecal matter, fossils of which are preserved as coprolites.

Fecal matter is rarely preserved in the Cambrian. However, in a few assemblages, the diversity and development of fecal matter are observed. There was little fecal matter available at the onset of the Cambrian, while larger and more diverse fecal matter became available by the middle Cambrian.

We assess the effect that increased availability of fecal matter had on deeper water environments and how this made such environments habitable for Cambrian organisms.

Combining these observations with data on digestive tracts and biogeochemistry of nutrient cycling in the Cambrian demonstrates that fecal matter played a significant role in driving the Cambrian Radiation.

The origin of fecal matter

Trophic interactions between animals have been suggested as a key driver for the **Cambrian** Radiation (see Glossary) [1,2]. While animals make their first appearance in the fossil record sometime around 600 Ma ago [3], many of the **Ediacaran** organisms are problematic to interpret and are of uncertain affinity and paleobiology. While the earliest animals appear this deep in the fossil record, few Ediacaran animals show evidence of guts [4,5] and there are currently no **coprolites** known from **Proterozoic** deposits. Coprolites are a subset of **bromalites** that reflect material extruded from an animal's digestive system [6,7]. They are the fossilized excrement of invertebrate and vertebrate animals and occur in many forms, such as fecal pellets, strings, and digested bioclasts [7,8].

In contrast to the Ediacaran, Cambrian coprolites have been reported from 36 deposits (Figure 1A; see also Table S1 in the Supplemental information online), ranging from the **Fortunian** (~538.8 Ma) to at least the **Paibian** (~494.2 Ma), and in the last 20 years, their ecological potential has been explored [9–13]. The deposits were identified based on a literature search using keywords including coprolite, fecal matter, feces, fragments, pellets, and bromalite. The search was conducted in English, German, and French using Google Scholar, Google, the Biodiversity Heritage Library, and by reviewing the cited literature in the recovered articles. Articles in other languages mentioning coprolites were translated using DeepL.

The lack of Ediacaran and very few early Cambrian coprolites might represent a bias, as there are few **Konservat-Lagerstätten** in this time frame. However, Cambrian coprolites are also known from ordinary fossil deposits (Table S1). An anthropogenic bias is more likely, as most research in this time frame concentrates on Konservat-Lagerstätten-type deposits, and the known early coprolites are all from the microfossil record (Figure 1A and Table S1).

Coprolite morphology and preservation vary significantly across the Cambrian (Figure 1B–M and Table S1). They range from microscopic to several centimeters in size and include forms such as

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elongated cylindrical, ellipsoid, circular, and 'exploded' fecal 'carpets', suggesting a multitude of producers, most of which are unknown. The shift in the coprolite record coincides with a change in feeding behavior among organisms. The diet of Ediacaran organisms ranged from extracting plankton and particulate organic matter from the water column, grazing on microbial and algal mats, to scavenging, with the first evidence of predation found in the terminal Ediacaran [2]. These trophic interactions began shifting in the Cambrian, and by **Cambrian Stage 3,** the trophic dynamics were broadly similar to those of modern ecosystems [2].

Cambrian coprolites were mentioned as early as the 19th century [14]. However, coprolites from Cambrian **Fossil-Lagerstätten** [15] were only identified in the late 20th century [16–18]. Furthermore, the potential for ecological interpretations of coprolites within Cambrian Fossil-Lagerstätten has only recently been exploited [9–13].

Classification of Cambrian coprolites

It is important to understand the different kinds of coprolites present in the Cambrian, as they can provide information on the size and type of the producer, as well as insights into the Cambrian food web. The following classification scheme follows the consensus on the known Cambrian coprolites and provides an intuitive way to classify them. This scheme should be bolstered with facies-based descriptions of the depositional environment to provide context for the coprolites.

Cambrian macroscopic coprolites (Figure 1B–G), usually more than 1 mm in diameter, are the most common specimens. They include most named trace fossils, the majority of coprolites preserving shelly fragments, and all the coprolites preserved in backfilled worm or arthropod burrows that were made by deposit feeders. They are the easiest to prepare and identify, have a substantial record, and are subcategorized into five groups.

Macro-Group 1 (Figure 1B–D): Shelly coprolites. These are coprolites preserving remains of biomineralized fossils on the surface or in burrows. Fossils are usually fragmentary, and typical fossil remains include worm cuticle, trilobite, agnostoid, hyolith, echinoderm, sponge, bradoriid, and other bivalved arthropod fragments [9,12,19]. These fossils have typically not been assigned to **ichnogenera**.

Macro-Group 2: Two-dimensional organic pellets. These are preserved through **kerogenization** as carbonaceous films—coprolites preserving flattened, subcircular to elongated fecal pellets, referable to the ichnogenus *Coprulus* Mayer, 1952 [20]. These include surficial isolated pellets, surficial pellet aggregates, and dislodged pellet aggregates [12,19,21]. Some of these specimens have been referred to the ichnogenera *Alcyonidiopsis* Massalongo, 1856 [22] (senior synonym of *Tomaculum* Groom, 1902 [23,24]), *Planolites* Nicholson, 1873 [25], and *Cilindrotomaculum houi* Chen and Erdtmann, 1991 [7,19,26].

Macro-Group 3 (Figure 1F): Two-dimensional organic fill—coprolites preserving structureless organic fill and carbonaceous films in burrows. These include burrows filled with organic matter and specimens referred to the ichnogenera *Lumbricaria yunnanensis* Luo and Hu in Luo *et al*., 1999 [27] and *Spirodesmos milanai* Aceñolaza, 2005 [7,12,19,28].

Macro-Group 4 (Figure 1E): Three-dimensional pellets. These are coprolites that preserve three-dimensional fecal pellets, either as isolated pellets, trails, or burrows. The pellets are sometimes referred to the ichnogenus *Coprulus*, and when they are fecal strings or elongated aggregates consisting of subcircular fecal pellets lacking shelly fragments, they are referred to as *Alcyonidiopsis* [7,24].

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Macro-Group 5 (Figure 1G): Mixed coprolites, a combination of shelly fragments and organic matter. These coprolites preserve animal fragments, fecal pellets, or organic films. They can contain any of the aforementioned fills and are usually not assigned to ichnogenera [9,12].

Conversely, microscopic coprolites, usually less than 1 mm in diameter, are found as (i) phosphatic micro-coprolites, secondarily phosphatized by amorphous apatite, and (ii) small carbonaceous coprolites. Phosphatic micro-coprolites represent diverse Cambrian coprolites. They are currently known from nine deposits (Table S1 and Figure 1) and can be subcategorized into three groups.

Micro-Group 1 (Figure 1H–J): Three-dimensional pellets. These are coprolites composed of three-dimensional fecal pellets, either as isolated pellets, trails, or burrows. These pellets are sometimes referred to as ichnogenus *Coprulus*, and if found in fecal strings or elongated aggregates consisting of subcircular fecal pellets that lack shelly fragments, they are referred to as *Alcyonidiopsis* [7].

Micro-Group 2 (Figure 1K): Shelly coprolites. Phosphatic micro-coprolites composed of bioclasts are rare compared with fecal pellet micro-coprolites and macroscopic shelly coprolites. They are known from limited deposits [11,29,30] and are usually composed of a single type of bioclast, some of which include worm sclerites, bradoriid carapaces, and brachiopod valves.

Micro-Group 3: Mixed coprolites. Coprolites that preserve both bioclasts and fecal pellets. These coprolites contain bioclasts held together by fecal matter [30,31].

Cambrian-aged small carbonaceous coprolites (Figure 1L, M) are the rarest coprolites. This rarity reflects their delicate nature, low preservational potential, and the limited publication record of **small carbonaceous fossils**. To date, small carbonaceous coprolites are only known from four deposits (Table S1), but they represent the earliest types of coprolites known from the lowermost Cambrian [32]. These coprolites are preserved as flattened fecal strings, often containing subcircular fecal pellets (usually of consistent size), and specimens range from submillimeter size to about 2 mm in length. Fecal strings can be straight, coiled, looped, filmy, or sinuous. None preserve any recognizable animal remains [32–35].

Cambrian coprolites provide us with insights into how fecal pellets contributed to particulate organic carbon (POC) and the biological pump during the Cambrian Radiation and in deep time, and how their importance continuously increased (Figure 2).

Evolution of guts in the Ediacaran and Cambrian

The earliest described gut contents in the fossil record belong to tube worm-like *Calyptrina* Sokolov, 1965 [36] and mollusk-like *Kimberella* Glaessner and Wade, 1966 [37]. These fossilized gut contents are about 558 million years old and have been identified by biomarkers [5]. Few Ediacaran animals are known to preserve guts [4,5], and the only confirmed Ediacaran bilaterian through-gut that has been described belongs to cloudinomorphs from the uppermost Ediacaran [4] (Figure 3). The gut morphology of the cloudinomorphs is very simple—a straight cylindrical gut that connects a mouth to the anus—whereas the exact morphology of the *Kimberella* and *Calyptrina* gut is unknown. It is also unknown if any of these taxa were capable of producing fecal pellets. However, biomarker analyses concluded that *Kimberella* likely fed on microbial and algal mats, and *Calyptrina* was likely a suspension or detrital feeding organism (Figure 3) [5].

Glossary

Biological pump: the process by which organic matter in the ocean descends from the surface layers to deeper waters.
Bromalites: fossilized remains of material from the digestive system of organisms. They include material that has been excreted, regurgitated, or is still in the digestive tract.
Cambrian: geological period that ranges from 539 to 485 million years ago.
Cambrian Series 2: a geologic series that ranges from 521 to 507 Ma.
Cambrian Stage 2: a geologic stage that ranges from 529 to 521 Ma.
Cambrian Stage 3: a geologic stage that ranges from 521 to 515 Ma.
Cambrian Stage 4: a geologic stage that ranges from 515 to 507 Ma.
Cololite: fossilized intestine contents or gut filling.
Coprolite: fossilized fecal matter.
Coprophagy: the consumption of feces.
Coprovore: an animal that consumes fecal matter.
Ediacaran: geological period that ranges from 635 to 539 Ma.
Fortunian: a geologic stage that ranges from 539 to 529 Ma.
Fossil-Lagerstätten: rock bodies that preserve an unusual amount of paleontological information either in terms of fossil quality or quantity. They typically contain exceptionally well-preserved fossils or unusually large quantities of fossils.
Ichnogenera: names used to identify and distinguish morphologically distinctive trace fossils.
Ichnology: the science of studying organismal traces.
Kerogenization: the process by which organic precursors are converted and volatilized into inert, geologically robust carbon compounds (e.g., kerogens), usually observed as two-dimensional carbon-rich fossil films occurring after rapid burial in anoxic settings.
Konservat-Lagerstätten: deposits defined by their fossil quality, often preserving fossils with minimal decomposition of soft tissues, resulting in the preservation of organic skeletal components, such as chitin, as well as connected or articulated structures.
Miaolingian: a geologic series that ranges from 507 to 497 Ma.
Paibian: a geologic stage that ranges from 497 to 494 Ma.

The earliest Cambrian has yielded little information on gut morphology, but hyolith fossils from the Terreneuvian of the Montagne Noire, southern France, preserve exceptional three-dimensional digestive tracts [38]. The abundant specimens from that deposit show ontogenetic variation in gut morphology and a more advanced gut than that of the Ediacaran cloudinomorphs. These hyoliths have a digestive system that is simple and U-shaped in the early ontogenetic stages and a digestive tract in which a straight anal tube and a straight gut with local zigzag folds are observed in the largest specimens [38] (Figure 3).

By **Cambrian Series 2,** several Fossil-Lagerstätten from Australia (Emu Bay Shale), China (Chengjiang Biota, Guanshan Biota, and Qingjiang Biota), and Greenland (Sirius Passet) provide insights into the guts of arthropods and other organisms [31,39–43]. Among the simplest Cambrian digestive systems are those of priapulid worms. In Cambrian priapulids, a straight cylindrical gut connects a teeth-bearing muscular pharynx to the anus [44]. Similarly, most basal panarthropods possess tubular guts without digestive glands [40]. The most advanced digestive systems of this time are found in stem and crown arthropods [40,42]. These early Cambrian arthropods had already evolved foreguts and digestive glands that increased the efficiency of food processing [40]. These advanced arthropod guts likely made it easier to digest larger and harder food particles [40,42,45]. While other extant animal lineages have digestive systems with digestive glands, there is no evidence that they had already evolved these in the Cambrian (Figure 3).

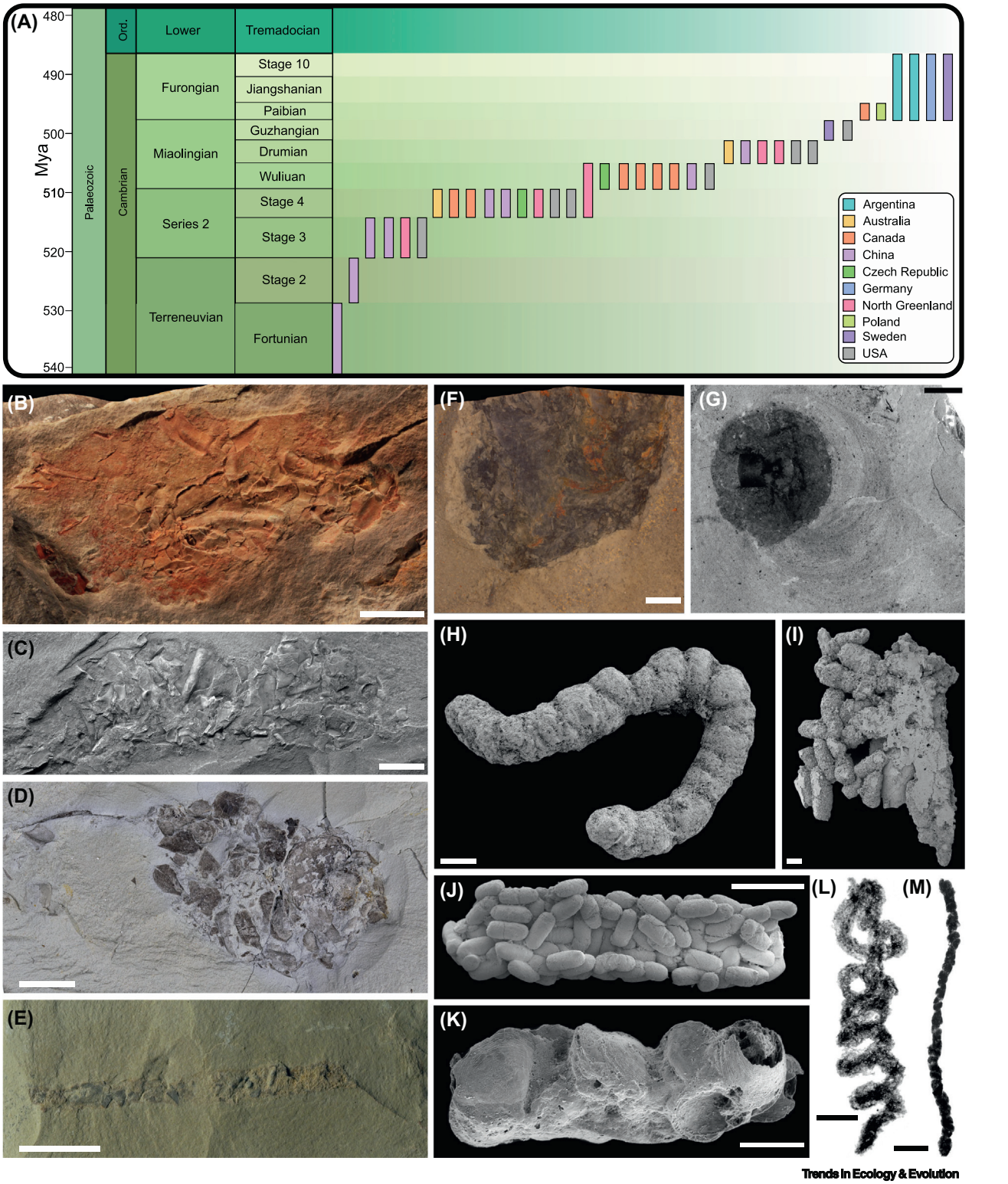
While the diversity of coprolites by Cambrian Series 3 suggests that a variety of digestive tracts were present to produce different coprolite shapes, it is only possible to understand the fecal matter morphology that is produced in **cololites**, as they link the fecal matter shape (pellet, string, etc.) to the digestive system [11,31,44,46].

The increased coprolite abundance in Cambrian Series 2, associated with larger coprolites containing skeletal debris [9] also correlates with the first major Cambrian Konservat-Lagerstätten [47] where animals with more advanced digestive tracts (Figure 3) had evolved [39,40,43]. Conversely, the absence of macroscopic coprolites in the Terreneuvian (Table S1) reflects the lack of larger early Cambrian animals. As such, the coprolite record tracks the evolution of guts during the Cambrian Radiation.

Potential producers

Cambrian coprolites are commonly composed of carbonaceous or organic material and/or bioclasts of benthic animals. This indicates that the coprolite producers frequently hunted and scavenged on the seafloor, as well as functioning as deposit feeders. This is supported by the identifiable coprolite contents, which usually include sessile animals (e.g., *Gogia* and sponges), benthic, likely slow-moving animals (e.g., hyoliths), priapulid worms, trilobites, and agnostids [9,12,19,48]. Additionally, some coprolites were produced by nektonic predators, as they preserve bivalved arthropod remains [9,12]. These invertebrate coprolites were likely produced by a different type of predator, and the most commonly suggested producers are radiodonts [49]. While many radiodonts were likely predators, as they possessed excellent eyesight, a crushing mouth cone, and raptorial appendages [50–52], it is unlikely that they produced most Cambrian coprolites. This is reflected in the preservation of coprolites in burrows [12,19,21] and the bioclasts in coprolites are morphologically comparable to the results of gnathobasic feeding, as opposed to twisting prey [12,13,29,53]. These coprolites were likely produced by benthic predators or scavengers (e.g., trilobites, priapulids, and annelids) and deposit feeders [9,12,19,54]. Other larger animals in Cambrian deposits are proposed as macroscopic coprolite producers, as bigger animals produce large fecal masses. Suggested taxa include aglaspidid arthropods,

Phanerozoic: a geologic eon that spans from 539 million years ago to the present day.
Proterozoic: geological eon that ranges from 2500 to 539 million years ago.
Small carbonaceous fossils: exceptionally preserved microscopic fossils of early animals, in whole or in part.



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chaetognath-like protoconodonts, *Fuxianhuia*, *Redlichia*, *Tuzoia*, and *Utahcaris orion* [49]. Unfortunately, most coprolites lack identifiable characteristics that could link them to a specific producer or group of producers [7].

The macroscopic coprolites from the Emu Bay Shale [13,55,56] may have been produced by the large trilobite *Redlichia rex*. This hypothesis reflects the observation that the trilobite has walking legs with stout gnathobasic spines [13]. Biomechanical modeling illustrated that this animal could have crushed shells using gnathobasic spines, similar to modern horseshoe crabs [57]. Gnathobasic spines could also have been used to tear soft-bodied organisms with a non-biomineralized cuticle. Indeed, modern horseshoe crabs fed a diet of small bivalves produce shelly feces with a morphology and angularity similar to Emu Bay Shale coprolites [13]. Bioclast-dominated coprolites may have been produced by other arthropods with gnathobasic-bearing walking legs. This hypothesis is also supported by the gut contents of the priapulid worm *Ottoia prolifica* Walcott, 1911 [58] from the Burgess Shale. In these rare specimens, trilobites are disarticulated, not crushed as they are in the Emu Bay Shale coprolites [44].

In rare cases, Cambrian organisms preserve gut contents [11,30,31,44,46]. These cololites provide the most accurate evidence of what Cambrian animals consumed. In many cases, the guts are filled with sediment rich in organic matter, suggesting that the animals had a detritivorous lifestyle [31,46]. Some of the most abundant cololites are known from the priapulid worm *Ottoia prolifica*, where over a third of reported specimens with gut contents preserved skeletal elements of hyoliths, brachiopods, trilobites, and bradoriids next to sediment. This suggests an omnivorous lifestyle similar to modern priapulids [31,44].

Most microscopic phosphatic coprolites are fecal pellets commonly lacking bioclasts or any overall identifiable characteristics of possible producers. This suggests that most microscopic coprolite producers were deposit feeders [11,29,30,59]. The limited amount of bioclasts in microscopic phosphatic coprolites are usually bradoriid valves or hyolith opercula [11,29,30,59]. Such specimens were produced by small predators or scavengers, such as a small arthropod or vermiform animal. Finally, small carbonaceous coprolites were likely produced by deposit feeders or grazers, as they are uniform subcircular pellets with no recognizable animal remains [34,35]. Unequivocal coprolites from planktonic filter feeders are currently missing in the Cambrian fossil

Figure 1. Cambrian fecal matter in time and space. (A) Deposits preserving Cambrian coprolites in time and space. Exact location and stratigraphic unit of the deposits can be found in Table S1. (B) Macroscopic coprolite preserving trilobite remains from the Emu Bay Shale, (Cambrian Series 2, Stage 4), South Australia, Australia. SAMA P54285. (C) Macroscopic coprolite preserving shell fragments from the Buen Formation (Cambrian Series 2), Greenland. PMU 22887. (D) Macroscopic coprolite preserving shell fragments and organic matter from the Wulongqing Formation (Cambrian Series 2, Stage 4) Yunnan Province, South China. YPM IP 421925. (E) Macroscopic coprolite preserving three-dimensional fecal pellets from the Ruin Wash Lagerstätte, Pioche Formation (Cambrian Series 2, Stage 4), Nevada, USA. CMC IPC 103497. (F) Macroscopic coprolite preserving unidentified organic matter from the Paseky Shale Member, Holšiny-Hořice Formation (Cambrian Series 2, Stage 4), Czech Republic. I261. (G) Spreiten-burrows associated with macroscopic coprolite, view from above containing valve (or valves) of the prey under worm cuticle (not discernible), with spreiten to the lower right from the Ravens Throat River Lagerstätte, Rockslide Formation (Miaolingian, Drumian), Canada. TMP 2013.101.0436. (H) Phosphatic microscopic coprolite from the Henson Gletscher Formation (Cambrian Series 2, Stage 4—Mioalingian, Wuliuan), North Greenland. MGUH 31218. (I) Phosphatic microscopic fecal pellets from the Aftenstjernesø Formation (Series 2, Stage 4), North Greenland. MGUH 31187. (J) Phosphatized microscopic fecal pellets from the Gaotai Formation (Miaolingian, Wuliuan) Guizhou, China. YKLP. (K) Phosphatized microscopic coprolite composed of shells from the Gaotai Formation (Miaolingian, Wuliuan) Guizhou, China. YKLP 12112. (L, M) Little Bear biota, Mount Cap Formation (Miaolingian, Wuliuan) Northwest Territories, Canada. (L) Small carbonaceous coiled fecal string. GSC 135511. (M) Small carbonaceous string of aligned pellets. GSC 135509. Scale bars: B, E: 10 mm. C: 2 mm. D, F, G: 5 mm. H, I: 100 microns. J: 500 microns. K: 250 microns. L: 75 microns. M: 450 microns. (F, G) Imaged under ethanol. Credit: C, H, I: John Peel; F: Petr Kraft; J, K: Xi-guang Zhang: L, M: Tom Harvey. Institutional abbreviations: CMC: Cincinnati Museum Center, Cincinnati, Ohio, USA; I: Horák Museum, Rokycany, Czech Republic; MGUH: type collection of the Geological Museum, Copenhagen, a part of the Natural History Museum of Denmark; PMU: paleontological type collection of the Museum of Evolution, Uppsala University, Sweden; SAMA: South Australian Museum Adelaide, Adelaide, South Australia, Australia; TMP: Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada; YKLP: Key Laboratory for Paleobiology, Yunnan University, Kunming, Yunnan, China; YPM: Yale Peabody Museum, New Haven, Connecticut, USA.

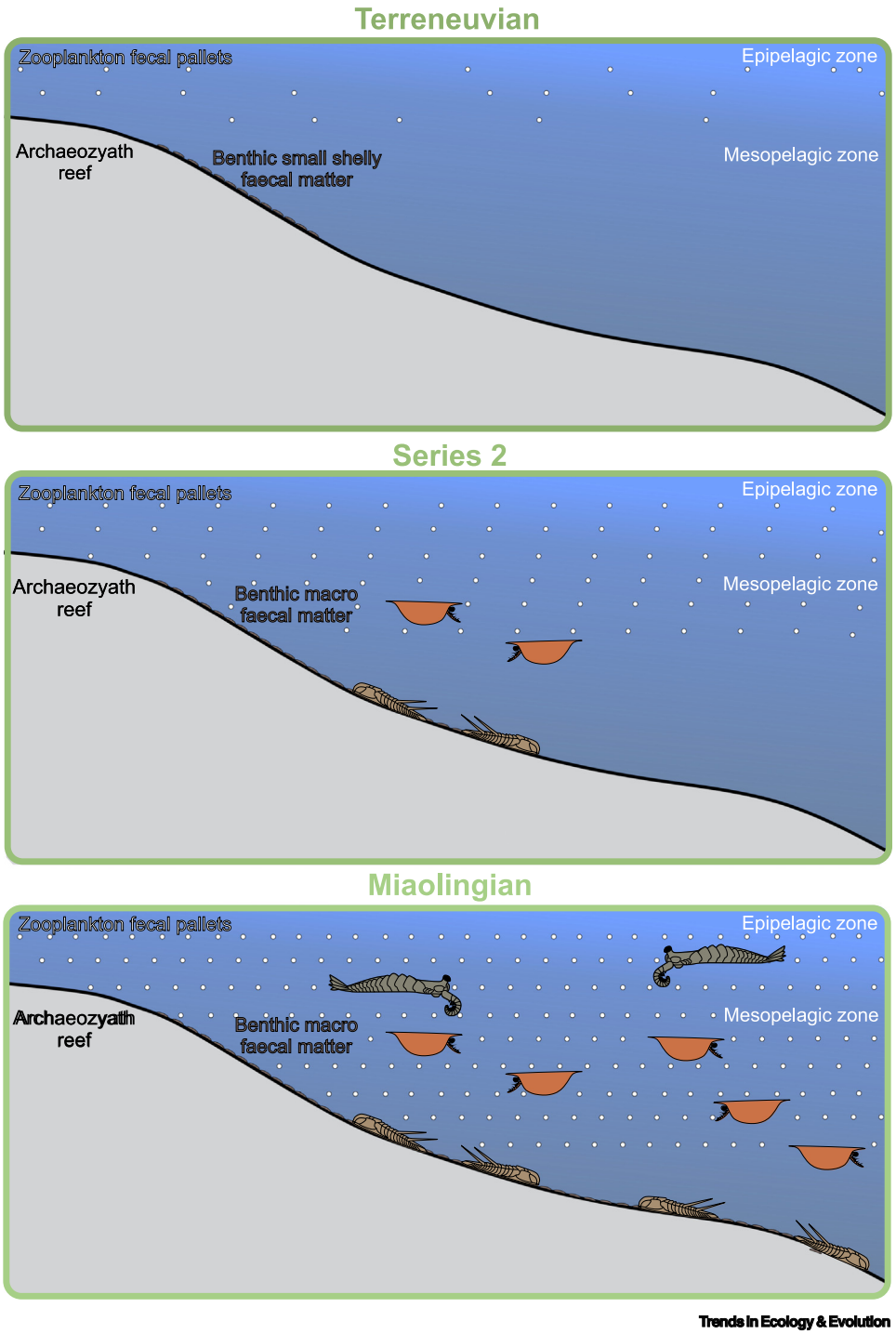

Figure 2. The increase and distribution of fecal matter in the Cambrian oceans during three key intervals.

record. This demonstrates how planktonic feces are very small and would easily dissolve into the water column before they are preserved, and that most planktonic feces would likely have been consumed before fossilization [60,61].

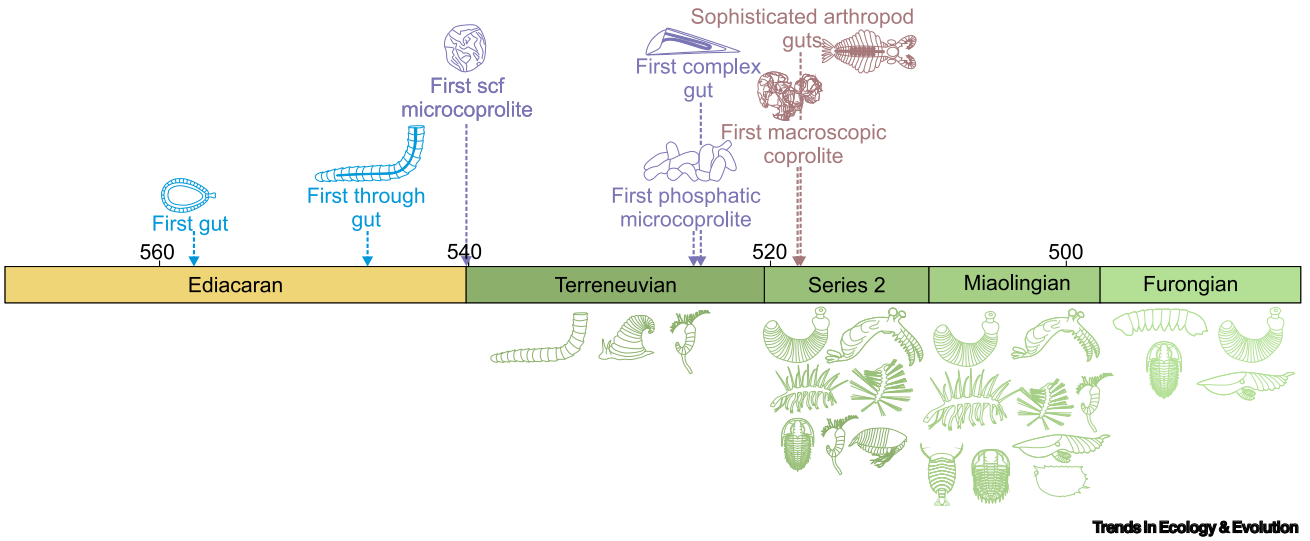

Figure 3. Key developments in fecal matter production in the Ediacaran and Cambrian. Top: Ediacaran to Cambrian biotic record of the first appearance of major evolutionary milestones and types of coprolites in the fossil record. Years are in mega-annum. Bottom: Illustrations of select potential coprolite producing clades in the Cambrian Series.

Trophic levels in the Cambrian

Over the last two decades, there have been major advances in understanding the biology of Cambrian animals [1,43,50–52,62,63], animal guts [39,40,44], coprolites and their producers [9,11–13,31], and trace fossil evidence [64–67]. This has resulted in the gradual untangling of trophic interactions in the Ediacaran and Cambrian marine ecosystems and has demonstrated that the general structure of modern marine food webs was established by Cambrian Stage 3 [1,2,9,39,40]. It has also been shown that the Cambrian food web was built on the foundation of the Ediacaran ecosystems [2].

The rise of modern trophic interactions in the early Cambrian coincided with major body plan shifts and resulted in an increased amount of biomass throughout the Cambrian and into the Ordovician [68]. By the middle Cambrian, these systems had become stable. Ecological changes accelerated the amount of fecal matter produced (Table S1). This, in turn, started a positive feedback loop in developing ecosystems, as fecal matter represents readily available organic matter, providing an important flux of carbon from surface to deeper water in oceans [60,61]. In modern oceans, most fecal pellets stay in the photic zone and are recycled by the activities of other animals or incorporated into the substratum. If they are large enough or become associated with aggregates, they might leave the photic zone and provide nutrition for organisms in deeper water [60,61].

However, several questions remain to be answered in Cambrian systems, as fecal matter in carbonate settings is poorly understood, even though deeper water carbonate muds were likely where large amounts of phosphatized fecal matter formed [69]. It can also be difficult to distinguish micritic peloids that could have had other origins (e.g., microbial) from true fecal pellets.

Fecal nutrients in the Cambrian

In modern oceans, particulate organic carbon (POC) moves from the euphotic zone into deeper water settings, driving the **biological pump**. Feces are an important nutrient in modern oceans

(Box 1) and a significant contributor to the POC, as well as to the iron (Fe), nitrogen (N), and phosphorus (P) cycles [73–75]. The modern POC is composed of a combination of fecal pellets from zooplankton and other animals, organic aggregates known as 'marine snow', and phytodetritus from sinking phytoplankton [61]. In modern oceans, the zooplankton fecal pellet contribution to the total POC can reach up to 100%, but usually remains below 40% [61].

The advent of fecal pellets across the Ediacaran/Cambrian boundary provided an additional source of organic carbon, as well as Fe, N, and P to deeper waters, likely resulting in more and different nutrients deeper in the water column. An increase in preserved organic carbon in shales of the early Cambrian has been observed [82,83] and while primary production would have played the major role, fecal matter undoubtedly increased the POC reaching the sediment. During the Cambrian, the amount of POC reaching deeper water must have constantly increased as biomass grew significantly and more animals with guts arose [68,83]. Increased zooplankton activity in the early Cambrian also coincided with the first evidence of larval trilobites, deuterostomes, and other animals [84]. With the abundance of microscopic Terreneuvian coprolites and increased records of coprolites from Cambrian Series 2 (Figure 1A and Table S1), there is strong evidence for a rapid increase in fecal matter production within the Cambrian ocean and, by extension, a striking acceleration of fecal matter abundance in POC. This does not indicate that the end-Cambrian nutrient cycle was identical to the modern system. Biogeochemical analyses of nutrients throughout the **Phanerozoic** have shown that lower Paleozoic nutrient cycles likely varied substantially from modern ones [78,85].

In addition to being rich in macro- and micronutrients, fecal pellets also make nutrients more bioavailable to organisms [70]. We can reasonably assume this was the case for early Cambrian fecal pellets. In this framework, fecal pellets significantly boosted support for marine animal life and possibly supported the diversification and increased Cambrian biomass.

Fecal nutrients also contributed to the earliest hotspots for N and P within Cambrian organisms. Dense aggregations of zooplankton can create these accumulations and positively affect primary production [73–75,86]. While this phenomenon is observed and tested in modern systems, nutrient cycling during the Ediacaran–Cambrian Period is less well understood [78,83,87]. As such, the effects of fecal matter on primary productivity remain hypothetical at present.

Box 1. Feces in modern marine ecosystems

Fecal matter plays a vital role in modern marine ecosystems, as it is rich in macro- and micronutrients, and is produced from zooplankton, macro invertebrates, and vertebrates [60,61,70–72]. It can positively affect primary production, as dense aggregations of consumers can create N and P hotspots [73–75]. Additionally, fecal matter can increase the bioavailability of certain micronutrients, serving as a food source for other marine animals [70,72,76]. Finally, fecal matter functions as a substrate for bacterial communities [71,73,77].

Zooplankton fecal matter plays a major role in the marine biological pump, functioning as it composes up to 100% of the POC in modern systems [61]. Zooplankton fecal matter is rich in C, N, and P and is central within these biogeochemical cycles, providing nutrients to shallow and deep marine settings [60,61,71,78]. Fecal matter also provides Fe to the global Fe cycle and moves biogenic Fe within the water column, delivering this element, which is essential for supporting many functional aspects of marine organisms, to mesopelagic communities [70]. It has also been suggested that the presence of certain species-specific fecal pellets can influence carbon fixation [76].

Fecal matter also provides direct nutrition to animals through **coprophagy**. This life mode is well documented in marine invertebrates and vertebrates and illustrates how fecal matter is an important food source for zooplankton, invertebrates, and vertebrates [70,72,79–81]. While nutrient content of fecal pellets varies greatly between genera and trophic guilds [79,81], they still contain higher concentrations of macro- and micronutrients than other food sources [80]. Many marine animals consume other species' fecal pellets [79,80], but zooplankton also consume a degree of its own produced fecal matter, resulting in recycling within their own system [60,61].

Box 2. Biota associated with Cambrian coprolites

Most Cambrian coprolites are isolated trace fossils that are not associated in proximity to other organisms. The most common fossils associated with coprolites are the fossil fragments preserved within coprolites. While most Cambrian coprolites are known from deposits preserving diverse biotas [9,19], which include soft-bodied and biomineralized animals—both possible producers—the data on the producers are more commonly not forthcoming, as multiple organisms in the biota could have produced the coprolites. In rare cases, a supposed producer is preserved close to the fecal matter or only one taxon could be the producer of the coprolites [13,54], but even such specimens only present a glimpse in the Cambrian ecosystem.

Rarely, coprolites are preserved with interpreted coprovores. This evidence provides important insight into Cambrian food webs. To date, the only Cambrian deposit where such feeding has been noted is the Ravens Throat River Lagerstätte [12]. Here, complete trilobites, agnostids, and hyoliths are preserved on the coprolites. This interaction has been interpreted as these forms consuming either the fecal matter or the microbiota that formed on the feces.

Vannier and Chen [9] documented many hyolith conches and trilobite fragments accumulated in circles around eldoniids and bivalved arthropods in the Chengjiang biota. Similar structures were also documented from the Spence Shale [88] and fecal pellets accumulating in a circular fashion around a burrow are known from the Ravens Throat River Lagerstätte [12]. The fragmented fossils exclude the possibility of an interaction between the animal in the center and fragments surrounding it, eldoniids, bivalved arthropods, and several vermiform organisms are potentially predatory and could have produced these structures [9,12]. This is further supported by the presence of arthropod carapaces and pieces of worm cuticle in the Ravens Throat River Lagerstätte [12]. However, they are most likely a 'postmortem' association, the aggregates likely resulted from bottom currents [9,12].

Conquering deeper water environments

The increased availability of fecal matter during the Cambrian Radiation (Table S1) was clearly a key component of increased POC reaching deeper water environments. This, in addition to increasing dissolved oxygen levels in the Cambrian ocean [83], resulted in marine shelves becoming more nutrient-rich environments, likely contributing to the biological diversification of Cambrian ecosystems.

The increased nutrient supply to the marine shelves would have provided resources for detritivore and bioturbator groups that invaded these environments during **Cambrian Stages 2–4** (529–507 Ma) [65–67,87]. The body fossil record also illustrates that more distal settings were colonized during this time [43]. The increased depth of the bioturbated zone would have resulted in a downward shift of the redox discontinuity surface, opening new ecological niches [64,66]. This allowed for the rise of **coprovores**[12] that took advantage of the availability of fecal matter (Box 2). By the **Miaolingian,** the marine shelf communities were well established and produced large amounts of fecal matter [12,19,34,53].

Concluding remarks

Most studies assessing the Cambrian Radiation focus on oxygen levels, biogeochemical cycles, feeding and food webs, predator–prey interactions, or the dynamics of functional feeding groups. The role of feces in early ecosystems is commonly poorly understood. The origin of fecal matter remains one of the most fundamental yet elusive questions in the evolution of animal life. Although the fossil record provides some insights into the rise of digestive systems and the earliest fecal matter, a clearer understanding of the oldest animals with guts and the types of early fecal matter they produced (see Outstanding questions) is needed. The early Ediacaran should be a focal point here, as this time period likely holds the key to understanding the ecology of the earliest ecosystems in Earth's history [89]. Integration of biogeochemical, **ichnological**, and morphological data offers a framework to better understand the Cambrian Radiation. These data should be examined within the context of fecal matter as a core driver behind early ecosystem colonization and niche partitioning.

Outstanding questions

When was the first fecal matter produced?

When and in what sedimentary setting and sediment type are the oldest feces preserved?

What did the earliest fecal matter look like?

What animal produced the earliest fecal matter?

What elements/nutrients was early fecal matter composed of?

Were there species-specific differences in the elemental composition of Ediacaran/Cambrian feces?

When did animals evolve through guts?

Are there late Tonian, Cryogenian, or early Ediacaran animals that had through-guts?

Which animal clade evolved the first through-guts?

Did through-guts evolve once or multiple times in the Neoproterozoic and Cambrian?

Were there more types and shapes of feces in the Neoproterozoic and Cambrian, and what implications do they have for animal physiology and metabolism?

When are modern levels of fecal matter in the particulate organic matter (particulate organic carbon) reached?

What was the percentage of fecal matter in the Ediacaran/Cambrian particulate organic carbon?

Which groups were the major contributors of fecal matter to the Ediacaran/Cambrian particulate organic carbon?

How biased is the Ediacaran/Cambrian coprolite record?

How many coprolites from other deposits have already been discovered but never published?

Have Ediacaran/early Cambrian coprolites been misidentified?

How was the earliest fecal matter preserved?

Is there a preservational bias for Ediacaran/early Cambrian coprolites?

Complex marine systems can only develop when a combination of temperature, nutrition, and biological drivers are present. Evidently, the ability of nutrients to be moved further from the shelf is central to the expansion of these systems. The rapid acceleration of organism size during the Cambrian Radiation increased coprolite size, which yielded a positive feedback loop, further accelerating the establishment of these ecosystems. It is evident that fecal matter played a much more important role than previously thought, and it is imperative that we move beyond considering coprolites as evidence for predator–prey systems and into a framework that explores their role in accelerating evolutionary innovation and ecological diversity.

Author contributions

J.K. and R.D.C.B. conceived and designed the study, wrote the manuscript, created the figures, and compiled the supplemental table.

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Declaration of interests

The authors declare no competing interests.

Declaration of Generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the authors used DeepL in order to translate publications written in languages other than English, German, and French. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Supplemental information

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